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Alien cyanobacteria *Anabaena bergii* var. *limnetica* Couté et Preisig from Lithuania: Some aspects of taxonomy, ecology and distribution

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ABSTRACT

The anthropogenic eutrophication of surface waters and the global climate warming promoted some bloom-forming tropical cyanobacteria, including *Anabaena*, distribution northwards. *Anabaena bergii* var. *limnetica* was for the first time recorded in Lithuania from the hypertrophic Lake Gineitiškės in 2008. It developed when the water temperature reached its annual maximum (July–August); its highest biomass (0.26 mg L^{-1}) was reached at the end of July. Akinetes formation started in the middle of August. The morphological variability of *A. bergii* var. *limnetica* morphospecies is presented. The morphological, ecological differences and distribution of *A. bergii* var. *limnetica* and the related morphospecies *A. bergii*, *A. bergii* f. *minor*, *Anabaena minderi* are discussed.

Introduction

Cyanoprokaryotes and algae disperse over the world in a natural way (via migrating birds, river basins, winds) as well as due to different human activities (ship ballast water, aquaculture, etc.) (Kristiansen 1996). However their establishment depends on favourable climate and habitat conditions for "travelling" species. The global climate warming has stimulated some tropical bloom forming cyanobacteria distribution northwards. Also, the anthropogenic eutrophication of surface waters caused the increase of toxic algal blooms world-wide. Akinetes, the resting cells of planktic nostocalen cyanoprokaryotes, help to withstand unfavourable conditions and play a key role in their invasion from lower to higher latitudes (Stüken et al. 2006). Temperature has a major impact on the competition between native and invasive cyanobacteria (Mehnert et al. 2010). Establishment of microscopic cyanobacteria and algae in the new territories and non-typical habitats could be described as invasion; however, this ascription is confusing due to insufficient studies of different species' ecological requirements. Cyanobacteria are often considered to be distributed world-wide. Nevertheless, cosmopolitan species exist only in the cases when the corresponding biotopes are widely distributed over the whole globe (Komárek and Anagnostidis 2005).

Anabaena bergii Ostenfeld is considered as an alien cyanobacteria in Slovakia, Germany and the Czech Republic (Hindák and Hindáková 2001; Stüken et al. 2006; Kaštovský et al. 2010). According to Hindák and Hindáková (2001), the appearance of *A. bergii* and of the morphologically similar *Anabaena minderi* Huber-Pestalozzi in freshwater gravit-pit lakes of Slovakia may be related to eutrophication and climate warming. Originally, *A. bergii* Ostenfeld and *A. bergii* f. *minor* (Kisseliov) Kossinskaya of similar morphology were described in the Aral Sea phytoplankton (cit. after Elenkin 1938; Gollerbakh et al. 1953).

A. bergii and its varieties, *A. minderi*, *Aphanizomenon ovalisporum* Forti and other similar cyanoprokaryotes having solitary trichomes narrowed towards the ends, with terminal cells maximum two times as long as wide previously belonged to the heterogenic "*Aphanizomenon gracile*" group into which species "transitional" between *Anabaena* and *Aphanizomenon* were included (Komárek and Anagnostidis 1989; Komárek and Komárková 2006). Based on the morphology supported by 16S rRNA analysis, the planktic coiled and straight *Anabaena* species has been transferred to the new genus *Dolichospermum*, while the benthic species remained in the genus *Anabaena* (Wacklin et al. 2009). Some former *Aphanizomenon* species were transferred to the newly established genus *Cuspidothrix* (Komárek 2010). So far, the taxonomy of *A. bergii* and related similar morphospecies has not been solved on generic level. Planktic filamentous cyanobacteria characterised by floating solitary metameric trichomes slightly narrowed towards the ends, with elongated akinetes in a paraheterocytic position, comprise one group – the *Anabaena*-like cluster B (Komárek 2010).

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Nevertheless, delimitation among some species within this group has already been done. The morphological features and size of the vegetative cells, heterocytes and akinetes of *Anabaena bergii* and *Aphanizomenon ovalisporum* overlap (Gkelis et al. 2005). Fergusson and Saint (2000) and Yılmaz et al. (2008) considered them as morphotypes of the same species. Stüken et al. (2009), upon comparing *A. bergii* and *A. ovalisporum* from different localities of the world, concluded that *A. ovalisporum* may be separated from *A. bergii* based on higher length–width ratio of its intercalary cells and the bluntly rounded form of apical cells. The morphological differences were confirmed by molecular data. *A. bergii* and *A. ovalisporum* joined in close, but separate clusters in the phylogenetic tree (Stüken et al. 2009). It was proved experimentally that the potentially invasive Mediterranean cyanobacteria *A. ovalisporum* could undergo a massive population growth in the higher latitudes under future climate conditions (Mehnert et al. 2010).

The taxonomy of *A. bergii* and related morphospecies is complicated. Different names are used by phycologists to identify smaller *A. bergii* specimens [*A. bergii* var. *minor* Kisselev, *A. bergii* f. *minor* (Kisselev) Kossinskaya, *A. bergii* var. *limnetica* and *A. minderi*]. Comparing the main diagnostic features of *A. minderi*, *A. bergii* var. *minor* and *A. bergii* var. *limnetica* Hindák (1992) assumed that these taxa are closely related or perhaps identical. Molecular data should be accepted as the basic criterion in modern taxonomy (Wacklin et al. 2009). However, at present, only *A. bergii* strains isolated from freshwaters are known (three from Europe, one from Africa and several from Australia) (Stüken et al. 2009). On the other hand, a correct classification is impossible without a careful combination of genetic data with morphological diversity and variation, ecological and ecophysiological characteristics (Komárek 2005). Morphological characters are important for practical use and identification of natural populations (Komárek 2010). The aim of this study was to provide detailed morphological data on the cyanobacteria *A. bergii* var. *limnetica*, for the first time recorded in a hyperthophic lake of Lithuania, as well as to review and discuss some aspects of its taxonomy, ecology and distribution.

Materials and methods

The morphology of *A. bergii* var. *limnetica* specimens from a polymictic small (0.24 km^2), shallow (mean depth 1.5 m) Lake Gineitiškės was studied during June–October 2008. The lake is located in the urban area of Vilnius environs (SE Lithuania) and belongs to the river Sudervė basin (area 52.1 km^2). Lake Gineitiškės is assigned to a hypertrophic type with low self-purification facilities (Klimas 1995).

Water samples were taken with a Ruttner bottle sampler from the surface (up to 0.5 m) water layer in the central part of the lake. Water temperature, pH, conductivity and transparency were measured *in situ* using a portable multiLine F/Set-3 meter (WTW) and a Secchi disk. A detailed description of the study area, lakes' physico-chemical characteristics and phytoplankton research data have been presented in Kasperoviciene et al. (2005). Both live and formaldehyde-preserved samples were used for a qualitative and quantitative phytoplankton examination with a light microscope, magnification 600×. 125 trichomes were measured to evaluate the size of *A. bergii* var. *limnetica* vegetative cells, terminal cells and heterocytes. Also, the morphometrical data of 60 matured and 30 young akinetes were evaluated also. Mean size values with average deviations are given in bold. The morphospecies morphology was documented by original drawings and pictures made with a Moticam 2300 digital camera. The paper is supported with tables summarizing the literature data on the morphology and occurrence of *A. bergii* var. *limnetica* and related morphospecies.

Results and discussion

Anabaena specimens with the filaments slightly narrowed at the ends and with conical terminal cells were found in a single locality, the hypertrophic Lake Gineitiškės, during study of a planktic cyanoprokaryotes in more than 30 Lithuanian eutrophic–hypertrophic lakes in 2008–2009. These cyabobacteria developed in the lake from the mid of July to the end of August, reaching the highest biomass (0.26 mg L^{-1}) at the end of July (Table 1). Water temperature varied from 20.4 to 23 °C and transparency from 0.45 to 0.5 m. *Microcystis*, *Anabaena*, *Aphanizomenon* and *Pyraminomas*, *Lepocinclis* prevailed in the phytoplankton during the *Anabaena* growth period.

The morphological features of *Anabaena* specimens from Lake Gineitiškės were similar to those of *A. bergii* f. *minor* (Kisseliov) Kossinskaya, *A. bergii* var. *limnetica* Couté et Preisig and *A. minderi* Huber-Pestalozzi. *Anabaena* trichomes in our study material were solitary, straight or slightly bent, narrowing at both ends, 78 – **201** ± **48** – 370 μm long (Fig. 1a). The filaments were shorter at the beginning of the development (181 ± 41.5 μm). Vegetative cells were pressed barrel-shaped with abundant aerotopes, length 2 – **3.5** ± **0.8** – 6 μm, width 3.8 – **4.3** ± **0.3** – 5.2 μm, length-to-width ratio 0.8. Terminal cells were 3.5 – **6.6** ± **1.5** – 11 μm long and 2.8 – **3.5** ± **0.3** – 4 μm wide, *L*:*W* ratio 0.9 – **1.9** ± **0.5** – 3.7. The majority of terminal cells had a typical conical shape (Figs. 1b–f, j–l and 2c); however, there were also slightly elongated cells with rounded (Fig. 1g, m–n) or blunted ends (Fig. 1h–i and o–p). Hindák (1992) had observed bluntly pointed or broadly rounded terminal cells in *A. bergii* var. *minor* from the Carinthian lakes. The shape of terminal cells of the *Anabaena* specimens studied sometimes differed at both ends of the trichome (Fig. 2b). One third of the filaments were broken. They usually break beside the heterocytes or akinetes and, as consequence, acquire typical intercalar vegetative cells at the end. Mucilaginous bridges between vegetative cells and heterocytes or akinetes were always seen. However, their shape was clear expressed only before filament break (Figs. 3j and 4n). Mucilaginous bridges were smaller than those attributed to *A. minderi* by Huber-Pestalozzi (1938: Fig. c–d, in p. 140) and resembled those of *A. bergii* var. *limnetica* (Couté and Preisig 1978).

Trichomes had commonly one (57% of filaments), occasionally two (35%), rarely 3–4 heterocytes. Sometimes two heterocytes in succession developed (Fig. 3e). Heterocytes were barrel-shaped to almost spherical, 5.8 – **6** ± **0.2** – 7 μm (Fig. 3). Akinetes formation in the *Anabaena* specimens started in the middle of August. Mostly one akinete (84% of filaments), sometimes two (16%), were found. They were separated from heterocytes by at least two vegetative cells (Fig. 2a). However, also heterocytes adjacent to akinetes were observed in *A. bergii* (Stüken 2007) and *A. minderi* (Tezanos Pinto and Litchman 2010). Young akinetes, green in colour, were 7–16 μm long and 4.5–9 μm wide (Fig. 4a). Matured akinetes were brownish-green, with smooth walls, 12 – **16.8** ± **1.9** – 23 μm long and 9.5 – **11.4** ± **0.8** – 13 μm wide, *L*:*W* ratio 1 – **1.5** ± **0.2** – 2. Their shape varied from cylindrical (65% of measured akinetes; Fig. 4b–d and k–l) to oval-elliptical (33%; Fig. 4e–i and m–o); also spherical akinetes were observed in a few occasions (Fig. 4j and p). According to Hindák (2000, 2001), the shape of akinetes is one of the main features distinguishing two closely related *Anabaena* morphospecies. Broadly oval to spherical akinetes are characteristic of *A. bergii* and longitudinally elliptical to cylindrical of *A. minderi*. The form of *Anabaena* akinetes in the Lithuanian lake population varied from that typical of *A. bergii* to that typical of *A. minderi*. Similarly, Hindák (1992) observed *A. bergii* var. *minor* with broadly to asymmetrically oval or cylindrical akinetes in Carinthian lakes. Akinetes of *A. bergii* from NE Germany lakes were broadly oval, spherical or cylindrical also (Stüken et al. 2006; Stüken 2007: Fig. 11d–e in p. 20). Though, it is obvious that the shape of akinetes alone is not a

Table 1
The abundance and biomass of *Anabaena bergii* var. *limnetica* and dominating species in phytoplankton of Lake Gineitiškės, 2008.

Date	Abundance, thous. units L^{-1} (% of total phytoplankton abundance)	Biomass, mg L^{-1} (% of total phytoplankton biomass)	Dominating species (% of total phytoplankton biomass)
VII 24	59 (0.11%)	0.17 (0.98%)	*Pyramimonas tetrarhynchus* 13.6%, *Lepocinclis* sp. 9.7%, *Romeria elegans* 8.6%, *Microcystis aeruginosa* 5.7%
VII 31	146.3 (0.69%)	0.26 (2.61%)	*Anabaena elipsoides* 11.4%, *M. aeruginosa* 11.1%, *Microcystis flos-aquae* 10.4%, *Microcystis viridis* 6% *Microcystis* spp. (single cells) 5.9%, *Aphanizomenon* sp. 5.1%
VIII12	193 (0.4%)	0.20 (0.98%)	*Pseudanabaena limnetica* 12.3%, *M. aeruginosa* 10.2%, *M. flos-aquae* 9.9%, *Aphanizomenon* sp. 9.6%, *Microcystis wesenbergii* 7.6%, *Anabaena flos-aquae* 5.4%

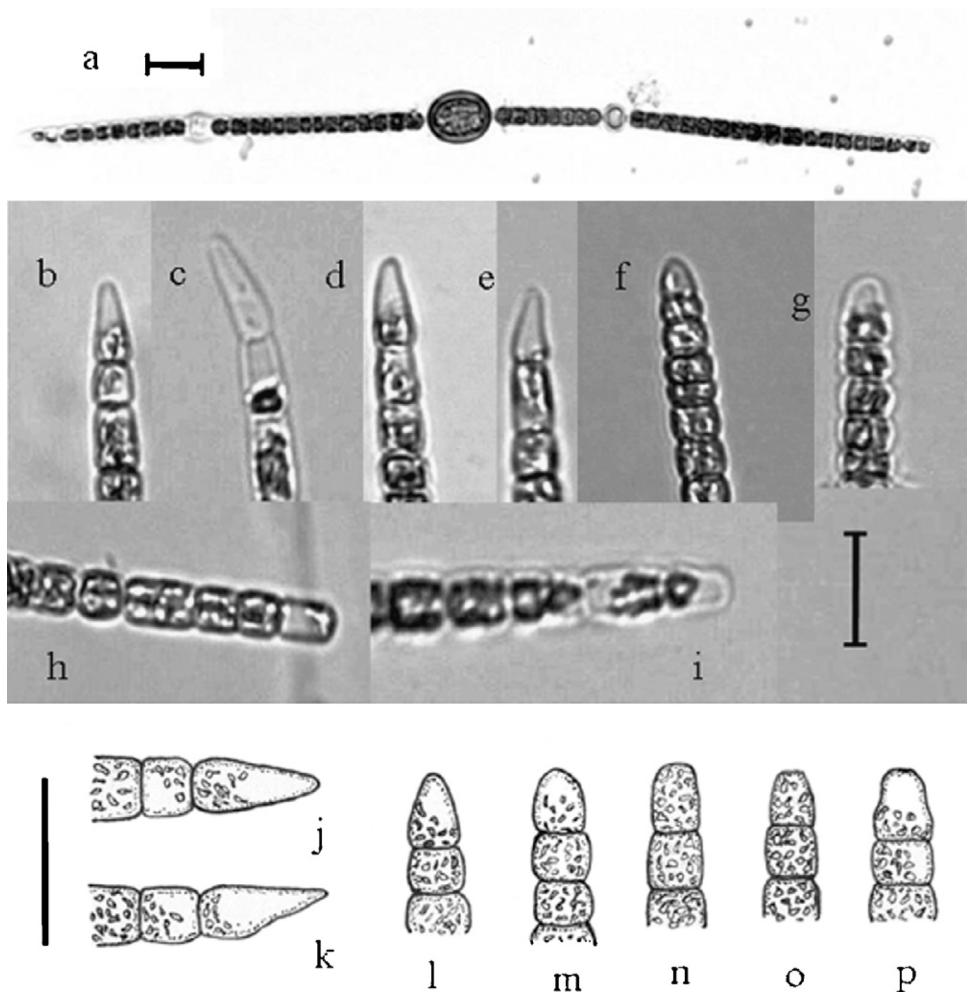

Fig. 1. The trichome (a) and terminal cells shape (b–p) of *Anabaena bergii* var. *limnetica*. Scale bar 10 μm.

feature sufficient to differentiate between the *A. bergii* and *A. minderi* morphospecies.

In addition to the shape of akinetes, the width of trichomes and the size of akinetes are diacritical features for differentiating among *A. minderi*, *A. bergii* and it varieties. The measurements of these morphospecies from different references are summarized in Fig. 5. Trichomes of *Anabaena* specimens from Lake Gineitiškės were narrower than those of *A. bergii* recorded from the Aral and Caspian seas (Ostenfeld 1906; Proshkina-Lavrenko and Makarova 1968). However, they were of similar width as *A. bergii*, *A. bergii* f. minor, *A. bergii* var. *limnetica* and *A. minderi* trichomes from the other localities (Fig. 5). The size of akinetes of *Anabaena* specimens from Lake Gineitiškės was similar to that of *A. bergii* f. *minor* from freshwater Lake Ostrovenskoe in Ukraine (Kondratjeva 1968). Akinete length of both specimens ranged within those recorded for *A. bergii* f. *minor* and *A. bergii* var. *limnetica* (Fig. 5). Actually, *A. bergii* var. *limnetica*, *A. bergii* f. *minor* and *A. minderi* from France, Switzerland and Austria freshwaters (Couté and Preisig 1978; Huber-Pestalozzi 1938; Hindák 1992) showed a close similarity in akinete size, and their length was prominently longer than in other morphospecies of this *Anabaena* group (Fig. 5). *A. bergii* var. *limnetica* was regarded as a synonym of *A. minderi* in some studies (Hindák 2000; Kaštovský et al. 2010), perhaps due to the priority of the description date. Their morphological differences from *A. bergii* are not sufficient to differ-

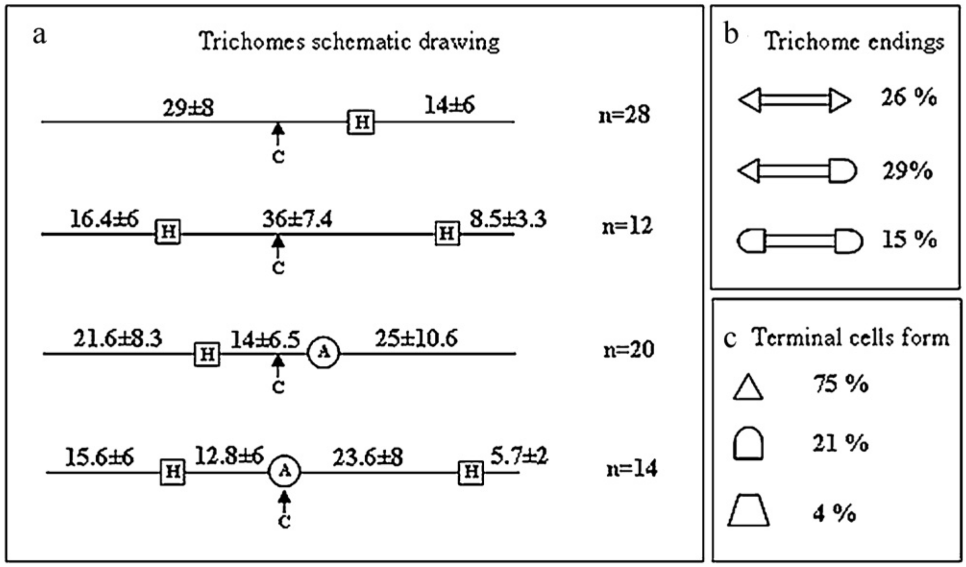

Fig. 2. Schematic drawing of *Anabaena bergii* var. *limnetica* trichomes structure (a), endings (b) and terminal cells shape (c); abbreviations: A – akinete, H – heterocyte, C – trichome center, n – number of filaments, figures above the line represent cell number, % – the percentage of measured filaments.

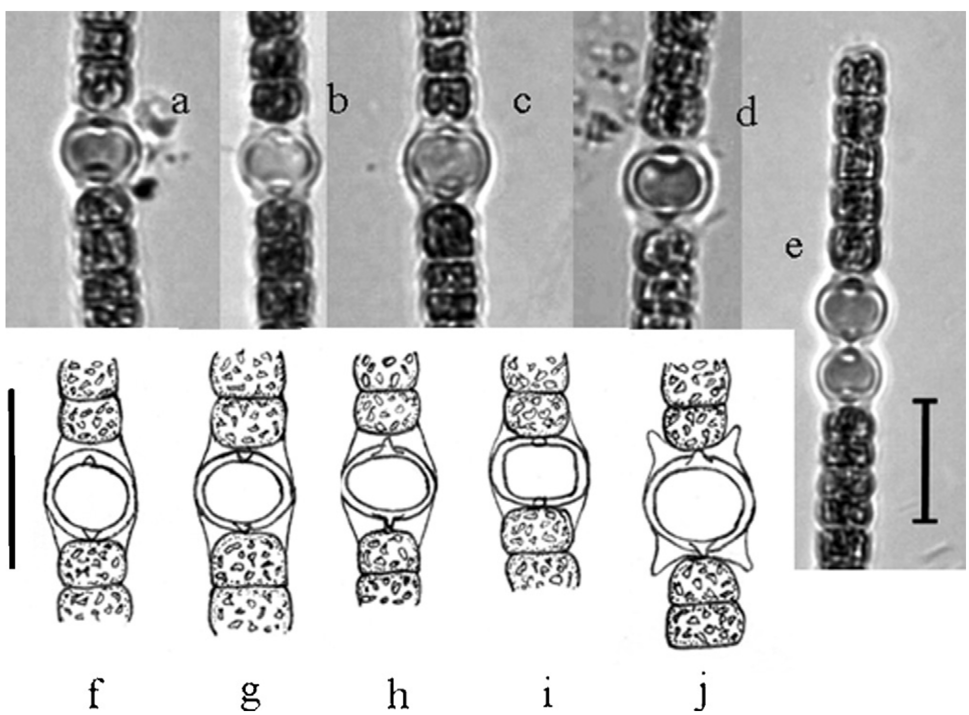

Fig. 3. The heterocytes shape of *Anabaena bergii* var. *limnetica*. Scale bar 10 μm.

entiate them on the species level, so probably *A. minderi* should be a synonym of *A. bergii* var. *limnetica*. Therefore, we have chosen the name *A. bergii* var. *limnetica* for the specimens from Lake Gineitiškės (Table 2).

A. minderi, *A. bergii* and its varieties occur in different types of water bodies, thus morphospecies distribution and ecological data require some consideration also. *A. bergii* Ostenfeld, 1908 and *A. bergii* var. *minor* Kisseliov, 1927 (the latter one is transferred to *A. bergii* f. *minor* (Kisseliov) Kossinskaya) were described from the phytoplankton of the Aral Sea (salinity ∼11 psu) which belongs to the Ponto-Caspian region. Later, they were recorded in the following saline-brackish environments of the Ponto-Caspian region: the Caspian Sea (5–12.5 psu), Lake Issyk-Kul (∼6 psu), the Black Sea (∼18 psu), the Tiligul lagoon (∼21 psu), the brackish Danube delta, Berezanska estuary, lakes near the Ural (4–40 psu) and relictic lakes in middle Asia (Table 3). Outside the Ponto-Caspian region, *A. bergii* and its variety were recorded in the hypersaline Bardawil Lagoon in Egypt (45–65 psu), inner Baltic Sea coastal waters (Saaler Boden, 1–3 psu), saline Slatina Pond in Serbia (∼1 psu) and Lake Phoosna in Pakistan (3.8 psu). On the other hand, these morphospecies were recorded also in freshwaters of Austria, Belarus, the Czech Republic, Egypt, Germany, Slovakia, Turkey, Ukraine and Senegal (Table 3).

The importance of salinity was first spotlighted by Couté and Preisig (1978). They assigned the smaller *A. bergii* specimens from

Table 2
Comparison of measurements of *A. minderi*, *Anabaena bergii* and its varieties.

Taxon/Reference	Trichome length, μm	Vegetative cell length (L) × width (W), μm	Terminal cell length × width, μm	Heterocyte diameter or length × width, μm	Akinete length × width, μm
***Anabaena bergii* Ostenfeld 1906**					
Ostenfeld, 1906 (cit. by Elenkin 1938)		≤8 × ±8	–	10	24 × 20
Proshkina-Lavrenko and Makarova (1968)	–	3.5–8 × 8–10(11)	6.6–10 × 3.3–5	7–9	20–25 × 10.5–19
Hindák (2000)	up to 400	5–7 × 5–7	–	7–8	14–18 × 10–15
Stüken et al. (2006) and Stüken (2007)	160–240	3–5 × 4–6 ($L < W$)	–	5–7	11–20 × 10–16
Çelekli et al. (2007)	–	W 6.5–8	–	10 × 10–10.5	–
Stüken et al. (2009) (strain LIE01AB)	–	4.4 ± 0.7 × 5.9 ± 0.6 ($L < W$)	12.5 ± 0.9 × 5.5 ± 0.8	8.0 ± 1 × 7.6 ± 0.5	–
Stüken et al. 2009 (strain LIE02AB)	–	3.9 ± 0.7 × 5.5 ± 0.4 ($L < W$)	12.4 ± 2.4 × 5.0 ± 0.8	7.6 ± 0.7 × 7.2 ± 0.7	–
Stüken et al. (2009) (strain ZIE26AB)	–	3.4 ± 0.9 × 5.1 ± 0.9 ($L < W$)	8.8 ± 1.3 × 3.8 ± 0.7	6.3 ± 1.3 × 6.4 ± 1.2	–
Stüken et al. (2009) (strain PMC215.03)	–	3.5 ± 0.7 × 3.8 ± 0.3 ($L < W$)	8.2 ± 1 × 2.8 ± 0.4	6.3 ± 0.7 × 5.3 ± 0.3	6.3 ± 0.7 × 5.3 ± 0.3
***Anabaena bergii* f. *minor* (Kisselev) Kossinskaja 1952 (=*Anabaena bergii* var. *minor* Kisselev 1927)**					
Kisselev, 1927 (cit. by Elenkin 1938)	–	W 5–6	–	6	15 × 11
Ulomsky, 1956 (cit. by Kondratjeva 1968; Couté and Preisig 1978)	–	3.4–4.5 × 4.5–5.8	6.8–14.4 × 3.4–5.1	6.1–9 × 6.5–8.5	13.6–20.4 × 10.8–15.1; L:W 1.2–1.4.
Proshkina-Lavrenko and Makarova (1968)	–	3–7.5 × 3–5	–	5.6–8	9–16 × 8–10
Kondratjeva (1968) (brackish)	–	W 4.2–6.5	–	5–6.5	13–16 × 11–12
Kondratjeva (1968) (freshwater)		W 4.2–6.5	–	5–6.5	13–25 × 11–14
Hindák (1992)	390–530	(2)–4–6 × 2.5–5	–	4–6 × 4.5	(8)–25–30 × (4)–8–12
Cvijan and Krizmanić (2009)	–	3.6–5.8 × 5.2–6.5	–	6–6.4 × 5.7–6.5	–
***Anabaena bergii* var. *limnetica* Couté et Preisig 1978**					
Couté and Preisig (1978) (France)	–	3–6 × 4–5	7.5–13 × 3–4	7 × 7–9	19–28 × 11–13; L:W 1.7–2.2
Couté and Preisig (1978) (Swiss)	–	2.5–6 × 3.5–5.5–(7)	5–15 × 2.5–4	7–8 × 7–9	19–32 × 11–13; L:W 1.7–2.5
Koreivienė and Kasperovičienė	78–201–370	2–3.5–6 × 3.8–4.3–5.2; L:W 0.8	3.5–6.6–11 × 2.8–3.5–4; L:W 0.9–1.9–3.7	5.8–6–7	12–16.8–23 × 9.5–11.4–13; L:W 1–1.5–2
***Anabaena minderi* Huber-Pestalozzi 1938**					
Huber-Pestalozzi (1938)	–	W 4–4.5–(5.2) ($L \leq W$)	–	5.2–6.5	23.4–25 × 10.4–13
Hindák (2000)	200–350	4.5–5.5 × 4.5–5.5	L: up to 10	6–8 × 5–10	12–20 × 9
Bucka and Wilk-Woźniak (2005), (personal communication)	196.9–375	W 4–6	–	–	15.6 × 10.9

–: no data.

Table 3
The recorded localities of *A. minderi*, *Anabaena bergii* and its varieties (* saline and brackish water bodies).

Country	Water body	Altitude, m	Area, km^2	Volume, 10^6 m^3	Depth, m		References
					Max.	Mean	
***Anabaena bergii* Ostenfeld 1906**							
Australia	Glenbawn and Tanunda Farm dam, Thornden reservoir	–	–	–	–	–	cit. after Stüken et al. (2009)
Belarus	Lake	–	–	–	–	–	Mikheeva (1999)
Czech R.	Recreational pond, sand-pit lakes	–	–	–	–	–	Kaštovský et al. (2010)
Egypt	*Bardawil Lagoon	−1–3	650	–	2.5	–	Konsowa (2007)
Germany	8 lakes and *coastal waters of Baltic Sea						Stüken et al. (2006), Stüken (2007) and Stüken et al. (2009)
	Petersdorfer See	–	0.24	0.45	3.8	–	
	Lake Petznicksee	–	0.72	–	2	–	
	Lake Melong	–	2.15	7.2	10	–	
	Lake Lieps	–	4.31	9.7	3.8	–	
	Zierker See	59	3.47	5.68	3.5	1.6	
Pakistan	*Lake Phoosna	50	2	–	–	2-3	Leghari et al. (2006);
Russia	*Aral and *Caspian Sea; *Lake Issik-Kul	–	–	–	–	–	Elenkin (1938), Gollerbakh et al. (1953) and Proshkina-Lavrenko and Makarova (1968)
Senegal	Guiers	–	300	600	–	2.0	Stüken et al. (2009)
Slovakia	gravel-pit lakes at Trávnik, Štrkovec,	–	–	–	–	–	Hindák (2000) and Hindák and Hindáková (2005)
Turkey	monomictic Lake Abant	1340	1.28	–	18	–	Çelekli et al. (2007)
Ukraine	*brakish Danube delta, bays, *Tiligul lagoon	–	–	–	–	–	Vladimirova and Danilova (1968), Terenko (2005) and Tsarenko et al. (2006)
***A. bergii* f. *minor* (Kisselev) Kossinskaya 1953 (=*Anabaena bergii* var. *minor* Kisselev 1927)**							
Austria	Lake Keutschacher	510	1.33	14.3	15.6	10.6	Hindák and Deisinger (1989) and Hindák (1992)
	Lake Hafnersee	506	0.16	–	10	5.1	
Egypth	Ain El-Mahabes	–	–	–	–	–	Hamed (2008)
Russia	*Caspian and *Aral Sea, relict lakes (middle Asia); saline lakes near Ural	–	–	–	–	–	Elenkin (1938), Gollerbakh et al. (1953) and Kondratjeva (1968)
Serbia	*Slatina Pond	–	–	–	0.9	0.5	Cvijan and Krizmanić (2009)
Ukraine	*brakish Danube delta bays,*Beresanska estuary	–	–	–	–	–	Vladimirova and Danilova (1968), Kondratjeva (1968) and Tsarenko et al. (2006)
	*Black Sea	–	–	–	–	–	Brjanceva et al. 2005
	Lake Ostrovenskoe	–	2.5	5.9	3.8	–	Kondratjeva (1968);
***Anabaena bergii* var. *limnetica* Couté et Preisig 1978**							
France	Barrage lakes of the rivers Seine and Marne	139–140	2.3–4.5	–	20	–	Couté and Preisig (1978)
Swiczer-land	4 ponds near Zurich	350–375	0.004–0.0124	–	3.9–5.6	–	Couté and Preisig (1978)
Lithuania	Lake Gineitiškės	133	0.24	–	2.5	1.5	Koreivienė and Kasperovičienė
Australia	Saline and freshwater lakes	–	–	–	–	–	Kemp (2009)
***Anabaena minderi* Huber-Pestalozzi 1938**							
Argentina	Shallow coloured lake	–	–	–	–	–	Tezanos Pinto and Litchman (2010)
Poland	*Lake Piaseczno	122	0.63	5.4	21.5	–	Bucka and Wilk-Woźniak (2005) and Mazurkiewicz-Boroń et al. (2008)
Slovakia	Gravel-pit lake at Dunajská Streda, at Jančikov dvor, Číčov, Vel'ký Draždiak, Štrkovec, Rohlík, 3 gravel-pit lakes at Čunovo, Rusovce,	–	–	–	–	–	Hindák (2000), Hindák and Hindáková (2002, 2003, 2005)
Slovenia	Lake Šmartinski	265	1.02	6	~10	4.9	Remec-Rekar et al. (2008)
	Lake Pernijško	245	1.23	3.4	~4.5	3	
	Lake Grajševsko	206	0.77	2.0	~10	<3	
Switzerland	monomictic Lake Greifen	435	8.5	150	32.2	17.7	Huber-Pestalozzi (1938)
Turkey	Hirfanli dam lake	856	280	5900	92	–	Baykal and Açikgöz (2004)

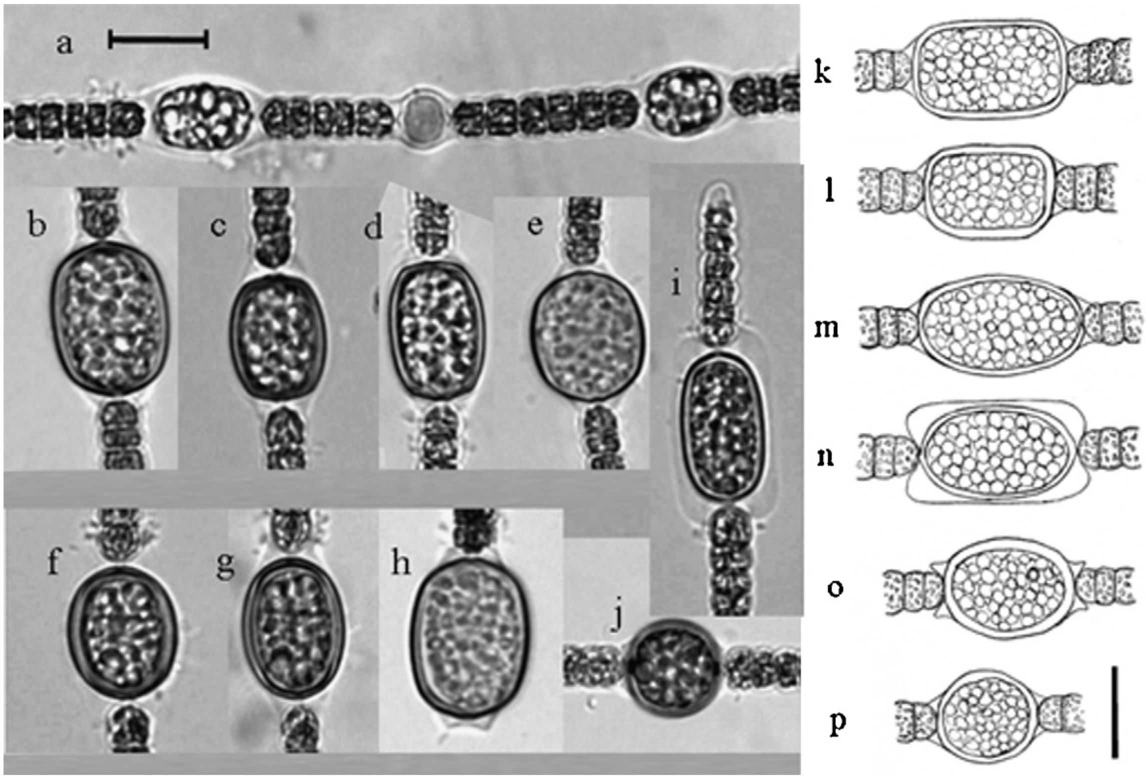

Fig. 4. The shape of young akinetes (a) and matured akinetes (b–p) of *Anabaena bergii* var. *limnetica.* Scale bar 10 μm.

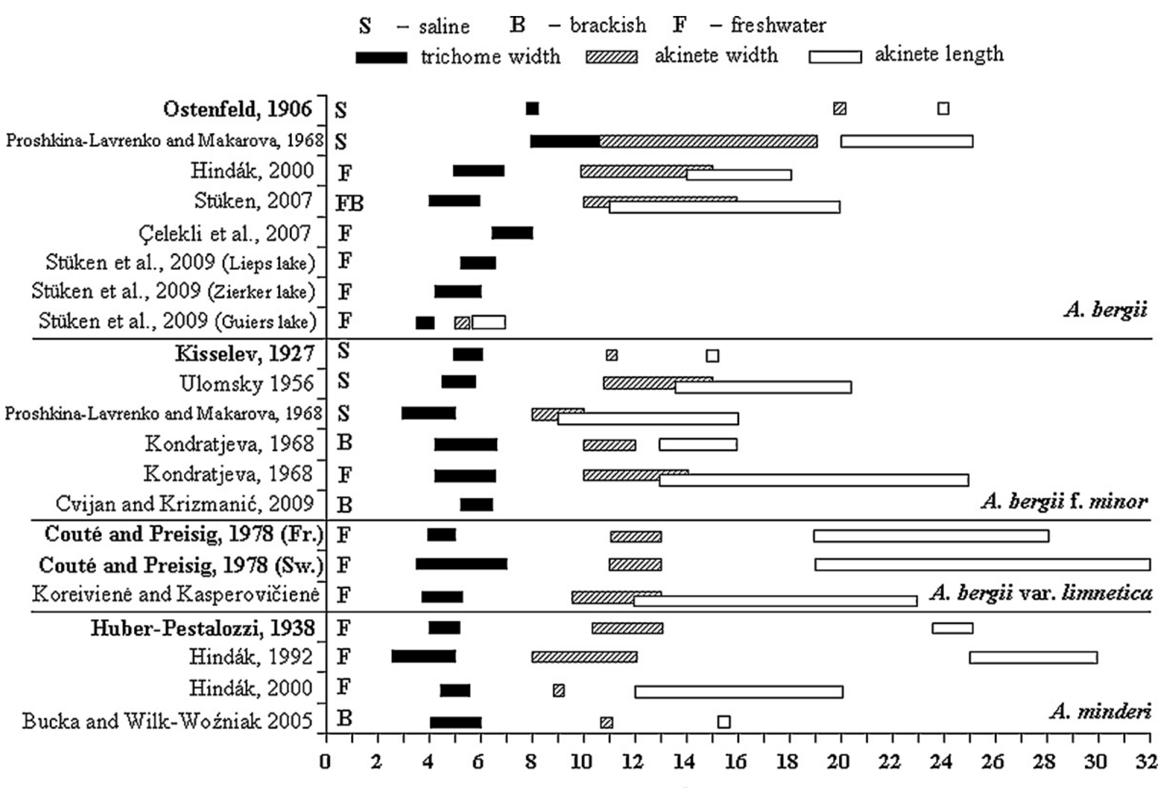

Fig. 5. Comparison of *A. minderi*, *Anabaena bergii* and its varieties trichomes width and akinetes dimensions according different references; references the morphospecies were described are given in bold.

freshwaters to a new variety *A. bergii* var. *limnetica.* They compared the morphology and ecology of *A. bergii* var. *limnetica* with those of *A. bergii* and *A. bergii* f. *minor*, but, did not include into discussion the morphologically similar *A. minderi* described by Huber-Pestalozzi (1938) from the freshwater pre-alpine Lake Geifen (Switzerland). Similarly, Huber-Pestalozzi did not give a morphological comparison of *A. minderi* with the previously described similar *A. bergii* Ostenfeld, 1906. At present, *A. bergii* var. *limnetica* is known from

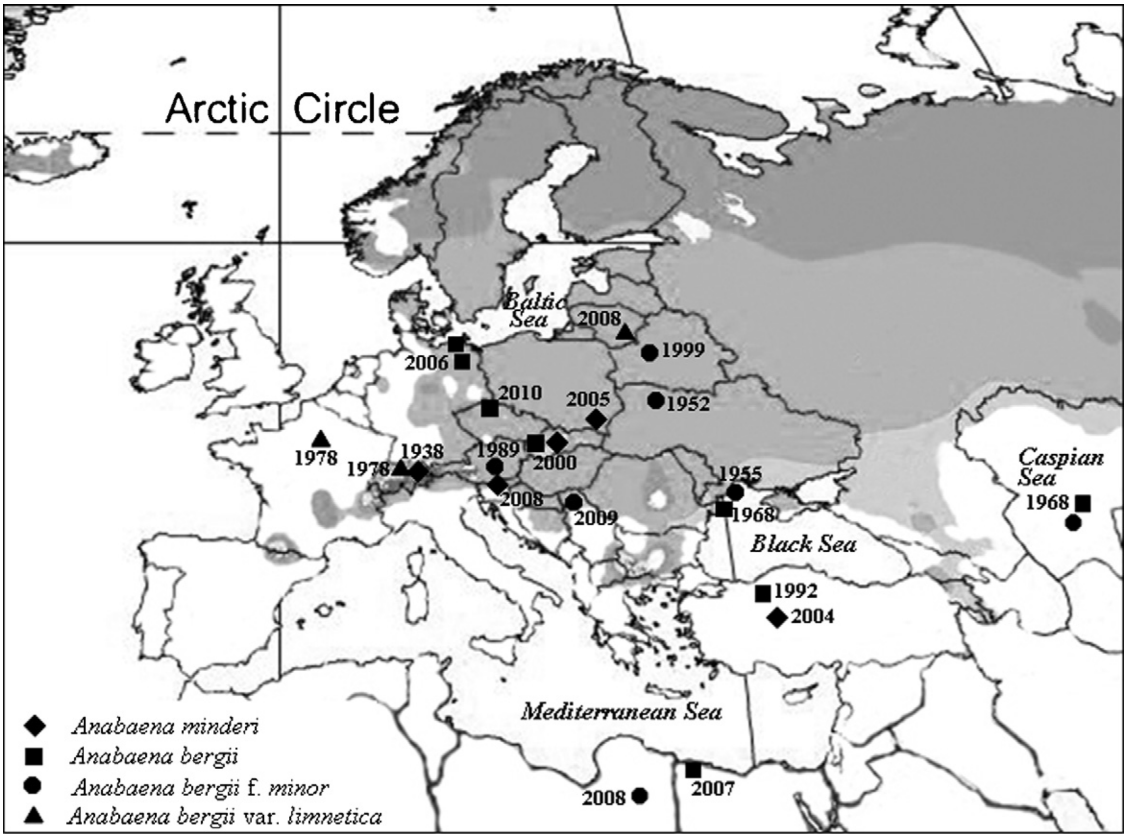

Fig. 6. *A. minderi*, *Anabaena bergii* and its varieties distribution in Europe and close proximity with date of species first record in different countries (Grey colour – Hemiboreal climate zone according to Köppen-Geiger classification system; Kottek et al. 2006).

freshwaters of France and Switzerland, as well as from fresh and hyposaline (up to 10 psu) waters of Western Australia (Kemp 2009). *A. minderi* was found in freshwaters of Argentina, Slovakia, Slovenia, Switzerland, Turkey as well as in hard water, rich in sulphates Lake Piaseczno in Poland (~1.2 psu) (Table 3).

Up to date, *A. minderi*, *A. bergii* and its varieties have been known from more than 70 water bodies. The majority of the records come from the Ponto-Caspian region and the Hemiboreal zone of Europe (Table 3 and Fig. 6). They tend to occur in lentic waters: glacial lakes, gravel-pit and newly filled barrage lakes, ponds located 50–1340 m above sea level. Water bodies considerably vary in surface area (0.004–300 km^2), water volume (0.45×10^6–5900×10^6 m^3), maximum depth (0.9–92 m), mean depth (0.5–17.7 m)(Table 3) and salinity (from fresh to 40 psu). These morphospecies localities most often tend to be small (area less than 5 km^2) and relatively shallow water basins (mean depth <5 m) (Table 3).

The southern inland migration corridor through the Danube and Rhine rivers could favour, similarly as in the case of invasion of the Ponto-Caspian macroinvertebrates (Karatajev et al. 2008), the outspread of *A. bergii* to European waters. Furthermore, migrating birds may deliver *Anabaena* akinetes to longer distances. For example, Lake Phoosna (Pakistan) is an important winter resting place for migratory birds from Siberia which is located close to the Ponto-Caspian region. Temperature and light intensity are the key factors that vary most among the geographical latitudes (Mehnert et al. 2010). The rising temperature and light intensity as a consequence of climate warming stimulate the spreading of non-native cyanoprokaryotes and algae to new territories. *A. bergii* var. *limnetica* recorded in a Lithuanian lake is the northernmost point of distribution of *A. bergii* and its varieties. In Lake Gineitiškės, *Anabaena* specimens started developing when the water temperature reached the annual maximum (20–23 °C), however, it was by 2 °C lower than the optimal growth temperature for *A. bergii* isolated from a freshwater lake in Germany (Mehnert et al. 2010). Temperature could determine *A. bergii* var. *limnetica* occurrence in a single locality of Lithuania and its low productivity (0.26 mg L^{-1}). The temperature seems to be of essential importance for the distribution of *A. bergii* and its varieties northwards, while nutrients play an important role in specimens' productivity. In Lithuania, *A. bergii* var. *limnetica* was found in small, shallow, highly eutrophicated lake with a low transparency. Hindák and Hindáková (2001) have noted that *A. bergii* and *A. minderi* occurrence in Slovakian lakes may be related to eutrophication. According to Stüken et al. (2006), *A. bergii* was frequent in 4 of 12 shallow German lakes with a low transparency and their biomass reached up to 24% of phytoplankton biomass. *A. minderi* shows high relative growth rates at low irradiance (Tezanos Pinto and Litchman 2010) and this fact may explain a more abundant these cyanobacteria development in eutrophic, low transparency lakes. *A. minderi* was abundant in the slightly eutrophic pre-alpine lake Greifensee in September (Huber-Pestalozzi 1938) and was fairly numerous at a depth of 2.5–5 m in June in Lake Piaseczno (Bucka and Wilk-Woźniak 2005). *A. minderi* biomass constituted 0.22–1.07 mg L^{-1} in Slovenian lakes in August; the highest biomass was found in the highly eutrophicated Lake Pernijško (Remec-Rekar et al. 2008); whereas *A. bergii* var. *minor* occurred in low abundance in clear-water Carinthian lakes in September (Hindák 1992). *A. bergii* has recently occurred in four mesotrophic lakes of the Czech Republic (Kaštovský et al. 2010).

Being similar in morphology, *A. minderi*, *A. bergii*, *A. bergii* f. minor, *A. bergii* var. *limnetica* occur in different habitats varying from deep saline seas to shallow freshwater ponds. The future revision of strains isolated from both fresh and saline environments, based on molecular methods, will preclude the taxonomical confusion of different *Anabaena* names and give an answer to the question whether the varieties do exist or they are just an expression of *A. bergii* morphospecies phenotypic plasticity in different environmental conditions. In future, the isolation of *A. bergii* strains from Lake Gineitškės and their experimental testing to salinity will be carried out.

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